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INFLUENCE OF THE COMPOSITION AND CONCENTRATION OF THE NUTRIENT SOLUTION ON PLANTS GROWN IN SAND CULTURES

BY
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INTRODUCTION

Since the recognition of the fact that the mineral content of the plant body is derived from the mineral constituents of the soil, the part which the soil solution takes in the nutrition of the plant has been the subject of numerous investigations by chemists, plant physiologists, and soil scientists, who have made large contributions to our knowledge in this important field. The early investigations of Knop and other plant physiologists showed conclusively that the elements which are essential to plant growth are carbon, hydrogen, oxygen, nitrogen, sulphur, phosphorus, potassium, magnesium, calcium, and iron. As most of this work was done before the development of the new chemical and physical theories, in regard to solutions in particular, the problems dealing with the absorption of these elements remain for explanation in the light of this new knowledge. The modern period of research in this field has thus been characterized by an intensive study of the absorption of nutrient elements by the plant. The earlier conceptions, which had a marked tendency to link each element with some specific physiological process or with the development of some morphological part of the plant, have been

largely discarded in view of the recent investigations, which have shown that plant growth is not a simple function of any any particular element, but is to a very large extent influenced by the combinations of elements in the solution from which the plant derives its nourishment. Thus while calcium may in certain cases act as a neutralizer of oxalic acid,[1] it exhibits a more general function of antagonism for salts of potassium, sodium, magnesium, and other salts which would be toxic if calcium were not present.[2] While this antagonistic function may be characteristic, it would seem from the experiments of Tottingham[3] that either this antagonistic action of calcium or the toxic effects of magnesium are influenced by the total concentration of the solution. Tottingham, therefore, concludes that the injurious effects of magnesium depend not only on the amount of calcium present but also upon the complex balance between all the salts in the solution. It follows that while the later investigations have undoubtedly given a wider conception of the rôle of the various nutrient elements, the exact relation which exists between the recognized nutrient function of these elements and the balancing function in the solution is not definitely known.

The part which the total concentration of the solution takes in the complicated problem of plant nutrition is by no means clear. On the one hand, the experimental evidence of Cameron[4] and his co-workers shows that the plant growing in water culture is not influenced to any extent by wide variations in the total concentration of the solution, a view which is further supported by the researches of Tottingham,[5] who concludes that nutrient solutions ranging from 0.01 per cent to 0.14 per cent do not affect the dry weight in the case of wheat grown in these solutions. A similar view is taken by Stiles,[6] who thinks that the individual variation of plants grown in water cultures is as large or larger than that which is often accredited to a variation in the compo-

[1] Schimper, Flora, vol. 73, pp. 207–261, 1890.

[2] Loew, Flora, vol. 75, pp. 368–394, 1892; and U. S. Dept. Agric. Bur. Plant Ind. Bull. 45, 1903; Osterhout, Bot. Gaz., vol. 42, pp. 127–134, 1906, and vol. 44, pp. 259–272, 1907.

[3] Tottingham, Physiol. Res., vol. 1, pp. 133–245, 1914.

[4] Cameron, Jour. Phys. Chem., vol. 14, p. 320, 1910.

[5] *Loc. cit.*

[6] Stiles, Ann. Bot., vol. 29, pp. 89–96, 1915.

sition of the solution. In decided contrast to the evidence cited above, we have the investigations of Hall, Brenchley, and Underwood,[7] who conclude, on the basis of their resnlts with barley plants grown in a standard solution of four different concentrations, that "the growth made by plants in the soil solution is in the main determined by the amount of plant food they contain," and that "the concentration of the nutrient solution within certain wide limits, irrespective of the total amount of the plant food available, is a factor in the rate of plant growth which varies directly though not proportionally with the strength of the solution in the particular nutrient or nutrients limiting the growth." The experiments of Shive[8] are of considerable interest in this connection. Wheat was grown in solutions of three different total concentrations, 0.1, 1.75, and 4.00 atmospheres, in terms of possible osmotic pressure. The solution used was the three-salt solution first used by Birner and Lucanus[9] containing $Ca(NO_3)_2$, $MgSO_4$, and KH_2PO_4. All possible sets of proportion of these salts were included for increments of change equal to one-tenth of the total possible osmotic pressure. As judged from the extensive quantitative data collected, Shive concludes that the growth of wheat plants in solutions of any given salt proportion is determined by the concentration of the medium.

In the course of some experimental work concerning the dropping of flowers by F_1 species-hybrids of *Nicotiana*[10] it seemed desirable to grow a considerable number of plants in sand cultures which would vary widely both as to the principal nutrient elements, nitrogen, phosphorus, and potassium, and as to the total concentration of all of the nutrient salts. The marked influence of the nutrient factors upon the growth of the plant has afforded an excellent opportunity for a somewhat detailed study of the influence of the composition and concentration of the nutrient solution upon the growth of one of the higher seedplants of herbaceous character.

7 Hall, Brenchley, Underwood, Jour. Agric. Sci., vol. 6, pp. 278–301, 1914.

8 Shive, Physiol. Res., vol. 1, pp. 327–396, 1915.

9 Birner and Lucanus, Landw. Versuchsstat., vol. 8, pp. 128–177, 1866.

10 Goodspeed and Ayres, Univ. Calif. Publ. Bot., vol. 5, no. 9, 1916.

The Use of Sand as a Culture Medium

The ease with which solutions can be prepared and subsequently analyzed has made the water-culture method especially desirable in investigations of the rôle of nutrient substances in plant growth. A solution has generally been recognized, however, to be otherwise undesirable as a medium for the growth of the higher plants, since the root system is kept, during the course of the experiment, in an unnatural environment. Thus, while this method serves admirably for analytical purposes, it seems probable that the plant thus subjected to an unnatural environment will suffer certain more or less serious physiological disturbances. In this connection, it is a well-established fact that the development of root hairs is much greater in sand than in water,[11] the resistance of the substratum favoring root-hair production.[12] Roots in general grow longer and thinner in water than in sand or moist soil. Hall, Brenchley, and Underwood[13] think that the more vigorous growth of barley in sand, as compared with water cultures, is due to more efficient aeration of the former. It would seem, therefore, that sand is preferable to water as a culture medium, since in sand cultures the physical conditions present about the root system more nearly simulate those found in the soil. It is still a question just what part these physical conditions may have in plant nutrition. Undoubtedly such physical reactions as capillarity[14] and adsorption[15] must be important factors, since both the absorption and availability of nutrient salts would be affected by these physical phenomena. Breazeale[16] has shown that the effect of concentration in sand cultures is very different from that in water cultures, the best concentration for wheat in water being three hundred parts per million, while in sand it is in the vicinity of two thousand five hundred parts per million, an effect which is no doubt largely due to the adsorption of certain salts or ions by the sand particles.

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[11] Schwarz, Bot. Inst. Tübingen, vol. 1, pp. 135–188, 1883.

[12] Snow, Bot. Gaz., vol. 40, pp. 12–43, 1905.

[13] *Loc. cit.*

[14] Bell and Cameron, Jour. Phys. Chem., vol. 10, p. 659, 1906.

[15] Schreiner and Failyer, U. S. Dept. Agric. Bull. 32, 1906.

[16] Breazeale, Science, n. s., vol. 22, pp. 146–149, 1905.

The physical effects of sand as a medium for plant growth have been shown recently in a striking manner by McCall,[17] who added to sand the solutions which Shive[18] used as water cultures, with the result that much larger quantities of the nutrient salts were required than when the same species of plant was grown in water culture. The sand-culture method was selected for the present work with the above evidence in mind, and also because the growing period of the tobacco plant is long and this method precluded the tedious changing of solutions necessary when the water-culture method was used.

Experimental Material

The plant which was used in the present series of investigations was a tobacco of hybrid origin derived from a cross between *Nicotiana sylvestris* (U. C. B. G. 69/09) and *Nicotiana tabacum* var. *macrophylla* (U. C. B. G. 22/07) and known in the University of California Botanical Garden as U. C. B. G. H38.[19] The plants to be used were raised from seed and were transferred as seedlings to the sand from the flats in which they were grown after carefully washing the roots free from adhering soil particles. In picking out seedlings from the flats care was taken to choose from the large number of plants available only those which were most nearly uniform with reference to size and general appearance. The plants were kept during the experiment in a well-ventilated greenhouse.

The sand used was a light-colored beach sand which on analysis by means of the acid-digestion method of Hilgard showed the following composition:

Fe_2O_3	0.592 per cent	P_2O_5	0.004 per cent
Al_2O_3	0.46 per cent	MgO	0.28 per cent
K_2O	Trace	CaO	0.06 per cent

The water-holding capacity was 22 per cent when saturated. The sand was prepared for the experiment by washing in a heavy stream of tap water which was allowed to percolate through

17 Unpublished work.

18 *Loc. cit.*

19 Setchell, Univ. Calif. Publ. Bot., vol. 5, pp. 1–86, 1912.

a column of the sand for a period of twenty-four hours. The excess of tap water retained by the sand was in turn washed out with distilled water. While this sand is inferior to the best grade of pure quartz sand in freedom from inorganic material, it is unable to supply available nutrient elements in sufficient quantity to cause any perceptible increase in growth (pl. 14). Two thousand gram portions of the sand treated as above were weighed into six-inch flower-pots which had been previously prepared by dipping them into melted paraffin. The paraffining effectually closed the pores and prevented the absorption of the culture solution by the pot.

Distribution of Nutrient Salts

The pots were divided into three different groups designated as series I, II, and III, each series consisting of twenty pots divided into groups of five pots each, and a duplicate in each case, making forty pots in all in each series. In series I, nitrogen, as $NaNO_3$, was the varying factor within each group, the weight of each of the other salts being held constant. Thus, in series I, the pots 1 to 5 in each of the four groups contained $NaNO_3$ as follows: 0.02, 0.2, 1.0, 2.0, 3.0 grams. In a similar manner phosphorus and calcium, as $Ca(H_2PO_4)_2$, were varying factors in series II, while in series III potassium, as K_2SO_4, was varied. As noted above, the twenty plants of each series were divided into four groups designated respectively as A, B, C, and D, each group consisting of five plants and a control for each. The weight of one varying factor remained the same in pots of like number through all four groups. Thus plants I A 1, I B 1, I C 1, and I D 1 each contained 0.02 grams of $NaNO_3$, and I A 2, I B 2, I C 2, and I D 2 contained 0.2 grams of $NaNO_3$. But from group A to D the weight of the other nutrient factors decreases, so that group D contains two-thirds, C one-half, and D one-fourth the weight of each of these nutrient factors as present in the A group. The effect of this distribution of salts is to give at least three important variables. First, the single nurient salt in increasing proportions from plant 1 to plant 5 in each group, and second, the factor of total concentration which decreases from group A

to group D in each series. The third important variant, the balance of salts in the solution, follows as a matter of necessity, since the single nutrient salt added in increasing quantities from plant 1 to plant 5 is added with uniform variation and in the same quantity in each group, while the quantities of the other salts, although constant within a group, are not constant within all

TABLE 1

WEIGHT IN GRAMS OF SALTS ADDED TO EACH POT CONTAINING 2000 GRAMS OF SAND

(In the following table the roman numerals indicate the series numbers, and the letters are those of the corresponding groups.)

Pot No.	$NaNO_3$, grams	$Ca(H_2PO_4)_2.H_2O$, grams	K_2SO_4, grams	$MgSO_4.7H_2O$, grams	Total concentration, grams	Pot No.	$NaNO_3$, grams	$Ca(H_2PO_4)_2.H_2O$, grams	K_2SO_4, grams	$MgSO_4.7H_2O$, grams	Total concentration, grams
IA1	.02	1.2	2.4	.96	4.58	IIC1	1.5	.02	1.2	.48	3.20
IA2	.2	1.2	2.4	.96	4.76	IIC2	1.5	.10	1.2	.48	3.28
IA3	1.0	1.2	2.4	.96	5.56	IIC3	1.5	.20	1.2	.48	3.38
IA4	2.0	1.2	2.4	.96	6.56	IIC4	1.5	1.0	1.2	.48	4.18
IA5	3.0	1.2	2.4	.96	7.56	IIC5	1.5	2.0	1.2	.48	5.18
IB1	.02	.8	1.6	.64	3.06	IID1	.75	.02	.6	.24	1.61
IB2	.2	.8	1.6	.64	3.24	IID2	.75	.1	.6	.24	1.69
IB3	1.0	.8	1.6	.64	4.04	IID3	75	.2	.6	.24	1.79
IB4	2.0	.8	1.6	.64	5.04	IID4	.75	1.0	.6	.24	2.59
IB5	3.0	.8	1.6	.64	6.04	IID5	.75	2.0	.6	.24	3.59
IC1	.02	.6	1.2	.48	2.30	IIIA1	3.0	1.2	.02	.96	5.18
IC2	.2	.6	1.2	.48	2.48	IIIA2	3.0	1.2	.10	.96	5.26
IC3	1.0	.6	1.2	.48	3.28	IIIA3	3.0	1.2	.20	.96	5.36
IC4	2.0	.6	1.2	.48	4.28	IIIA4	3.0	1.2	1.0	.96	6.16
IC5	3.0	.6	1.2	.48	5.28	IIIA5	3.0	1.2	2.0	.96	7.16
ID1	.02	.3	.6	.24	1.16	IIIB1	2.25	.8	.02	.64	3.71
ID2	.2	.3	.6	.24	1.34	IIIB2	2.25	.8	.10	.64	3.79
ID3	1.0	.3	.6	.24	2.14	IIIB3	2.25	.8	.20	.64	3.89
ID4	2.0	.3	.6	.24	3.14	IIIB4	2.25	.8	1.0	.64	4.69
ID5	3.0	.3	.6	.24	4.14	IIIB5	2.25	.8	2.0	.64	5.69
IIA1	3.0	.02	2.4	.96	6.38	IIIC1	1.5	.6	.02	.48	2.60
IIA2	3.0	.10	2.4	.96	6.46	IIIC2	1.5	.6	.10	.48	2.68
IIA3	3.0	.20	2.4	.96	6.56	IIIC3	1.5	.6	.20	.48	2.78
IIA4	3.0	1.0	2.4	.96	7.36	IIIC4	1.5	.6	1.0	.48	3.58
IIA5	3.0	2.0	2.4	.96	8.36	IIIC5	1.5	.6	2.0	.48	4.58
IIB1	2.25	.02	1.6	.64	4.51	IIID1	.75	.3	.02	.24	1.31
IIB2	2.25	.10	1.6	.64	4.59	IIID2	.75	.3	.10	.24	1.39
IIB3	2.25	.20	1.6	.64	4.69	IIID3	.75	.3	.20	.24	1.49
IIB4	2.25	1.0	1.6	.64	5.49	IIID4	.75	.3	1.0	.24	2.29
IIB5	2.25	2.0	1.6	.64	6.49	IIID5	.75	.3	2.0	.24	3.29

the groups of a series. Thus I A 5, I B 5. I C 5, and I D 5 each contained 3 grams $NaNO_3$, but the content of each pot in K_2SO_4 was 2.4, 1.6, 1.2, and 0.6 grams, respectively; hence the balance between $NaNO_3$ and K_2SO_4 is very different in each of the four pots. Table 1 shows the distribution of the salts in the three series and the total concentration in grams of the salts in each pot. The total quantity of nutrient salts was added to the sand at the beginning of the experiment.

The plants were placed in the sand June 15 and were harvested about November 1, the tops and roots being kept for the determination of dry weight.[20] It will be seen that the plant was allowed sufficient time to complete its natural period of growth, thus permitting certain observations of a quantitative nature as recorded in table 2.

PHYSIOLOGICAL EFFECT OF NITROGEN

Distribution of Salts in Series I

In series I nitrogen as $NaNO_3$ was the salt which was used in the same weights in all of the four groups A, B, C, and D, being present in pots 1 to 5 as follows: 0.01 g. (.001 per cent), 0.2 g. (.01 per cent), 1.0 g. (.05 per cent), 2.0 g. (.1 per cent), 3.9 g. (.15 per cent). The maximum weights of other salts were $Ca(H_2PO_4)_2$, 1.2 g.; K_2SO_4, 2.4 g.; $MgSO_4$, 0.96 g., in group A, while the minimum quantity of these salts as added in group D was 0.3 g., 0.6 g., and 0.24 g., respectively. The total concentration in this series ranged from 1.16 g. in I D 1 to 7.56 g. in I A 5.

Height in Series I

The height of each plant was measured at two different periods. The first measurement was made when the majority of the plants were just beginning to show the first signs of flower-bud formation. The second measurement was taken five or six weeks later, when most of the plants were in full bloom. The final height of the five plants in each group is shown graphically

[20] An accident to the roots while drying prevented the collection of further data on their dry weight.

TABLE 2

SUMMARY OF QUALITATIVE AND QUANTITATIVE DATA FOR EACH PLANT

(In the following table the roman numerals indicate the series numbers, and the letters are those of the corresponding groups.)

Pot No.	Height, cm.	Leaf length, cm.	Leaf width, cm.	Number leaves	Number flowers	Dry weight tops, gms.
IA1	2.5	7.6	3.7	6.	0.	1.12
IA2	4.5	9.6	4.7	7.	0.	1.60
IA3	8.	12.1	6.2	10.5	0.	1.56
IA4	57.5	13.8	9.5	17.	25.5	.....
IA5	45.5	20.8	10.2	17.5	24.	7.83
IB1	5.5	9.5	4.9	7.5	0.	1.29
IB2	3.5	8.6	4.1	7.	0.	1.40
IB3	8.	12.1	5.5	9.	1.	2.17
IB4	78.	18.8	9.5	17.5	29.	8.57
IB5	49.	19.9	10.1	17.5	21.	7.96
IC1	3.5	8.8	4.3	6.5	0.	.74
IC2	2.5	8.3	4.3	6.	0.	.79
IC3	4.5	11.2	5.6	7.	0.	1.65
IC4	94.	19.5	9.7	17.15	31.5	.....
IC5	74.	18.7	9.1	18.	29.	9.24
ID1	6.5	10.5	5.4	7.	0.	1.65
ID2	17.5	12.7	6.3	9.5	0.	1.53
ID3	59.5	15.8	7.8	15.	8.5	5.86
ID4	91.5	14.6	7.7	19.	34.5	11.12
ID5	66.5	17.3	8.6	18.5	21.5	7.60
IIA1	15.	12.9	6.4	12.	0.	2.09
IIA2	55.	18.5	8.4	15.5	14.5	6.21
IIA3	69.5	18.9	9.4	16.5	22.5	8.75
IIA4	87.	19.2	9.7	16.5	25.5	8.58
IIA5	73.	18.9	9.3	16.5	29.	8.60
IIB1	21.	13.1	6.1	12.	0.	2.71
IIB2	35.5	15.3	7.3	14.5	4.5	3.82
IIB3	43.	15.	7.4	14.	9.5	4.1
IIB4	97.	18.3	9.3	18.5	37.	9.3
IIB5	74.5	18.6	9.6	17.	23.5	7.76
IIC1	13.5	12.2	5.9	11.	0.	2.73
IIC2	27.5	13.9	6.6	12.	3.	3.22
IIC3	101.	16.5	8.2	17.5	34.5	8.20
IIC4	90.	17.3	8.9	17.	32.	8.66
IIC5	78.	17.1	8.3	18.	26.5	7.88
IID1	18.	12.8	6.	11.5	2.5	2.47
IID2	64.5	14.8	7.4	15.5	15.	5.83
IID3	74.	15.5	7.6	16.	19.5	6.27
IID4	83.5	14.2	7.5	17.5	28.	7.60
IID5	86.	13.9	7.2	17.	19.	6.75
IIIA1	56.5	16.7	8.0	14.5	6.5	4.65
IIIA2	82.5	20.	10.1	16.5	27.	7.88
IIIA3	62.	20.7	9.6	17.5	14.	6.97
IIIA4	74.	20.2	10.	17.	20.5	10.53
IIIA5	63.	22.1	10.5	17.	24.	8.11

TABLE 2—(*Continued*)

Pot No.	Height, cm.	Leaf length, cm.	Leaf width, cm.	Number leaves	Number flowers	Dry weight tops, gms.
IIIB1	81.5	19.9	10.1	17.	22.	8.18
IIIB2	87.	20.3	10.	17.5	24.	5.87
IIIB3	94.5	18.3	9.4	17.5	31.	8.4
IIIB4	83.	19.1	9.7	18.	26.5	4.86
IIIB5	77.5	18.8	9.7	17.	39.5	8.42
IIIC1	89.	18.	9.	17.	18.	6.58
IIIC2	102.	17.7	8.8	17.5	22.5	8.57
IIIC3	109.	17.4	8.9	18.	23.	9.4
IIIC4	88.5	18.5	9.2	17.5	25.	7.66
IIIC5	79.	17.2	8.8	18.	26.5	8.68
IIID1	89.	16.4	8.2	17.	14.	5.6
IIID2	103.5	15.1	7.8	18.	17.5	7.27
IIID3	100.5	15.9	7.8	17.5	16.5	6.96
IIID4	90.	16.5	8.2	17.5	23.	6.75
IIID5	66.5	17.5	8.7	17.5	19.	6.36

in figure 1. As two plants were given similar treatment in each case, the height as noted in table 2 is the mean of the height measurements of these two plants.

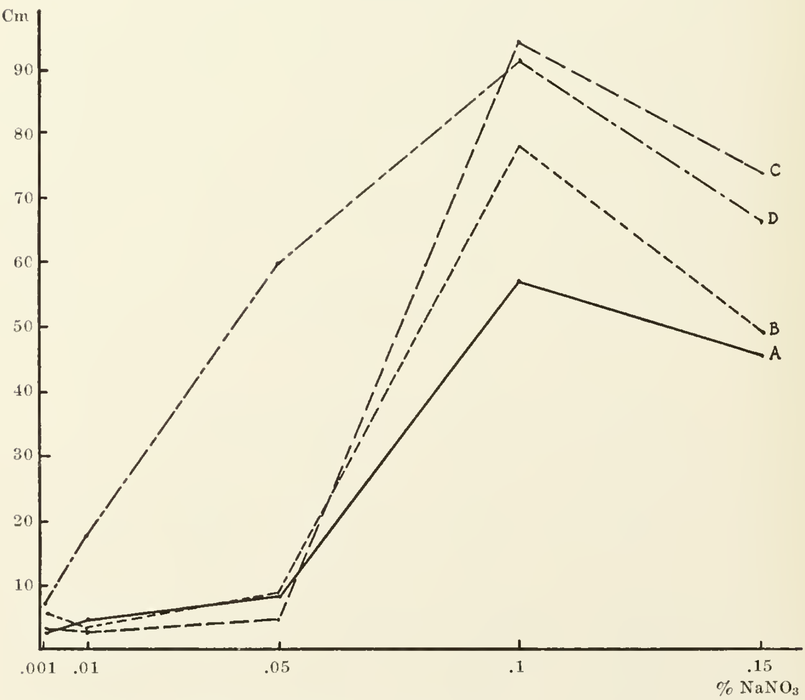

Fig. 1.—Graph showing the influence upon height of equal quantities of $NaNO_3$ in the different groups of series I.

The effect of increasing the quantity of nitrogen from plant 1 to plant 4 is marked in all groups. In every group plant 5 is not so tall as plant 4 (pl. 5), hence it would seem that the optimum nitrogen supply for tobacco growing in sand cultures, with height as an index, is somewhere near 0.1 per cent of $NaNO_3$, calculated on the basis of the dry weight of the sand.

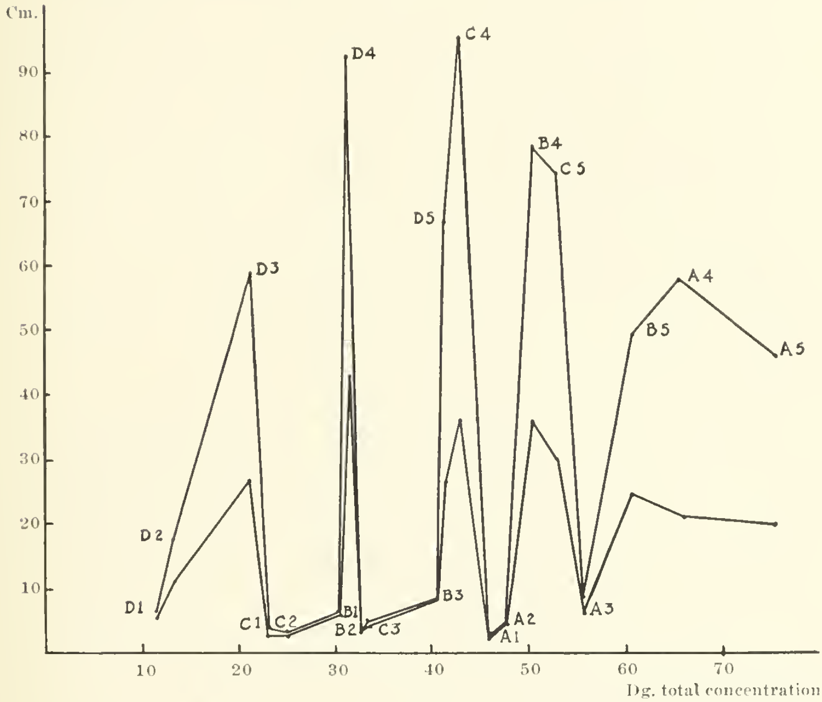

Fig. 2.—Graph showing the influence of total concentration upon height in series I.

There is slight variation in the first three plants of groups A, B, and C, showing that change in the total concentration of the solution within these limits does not affect the characters of the plants to any great extent. This, however, does not apply to group D, in which the total concentration is low (1.16 to 4.14 g.), for plants 2 and 3 are far superior to the corresponding plants of the other groups, although the nitrogen content is exactly the same. When the nitrogen content is at or near the

optimum the influence of concentration on height is exhibited in a more uniform manner, as shown in plants 4 and 5 of all groups (pl. 6). Plants growing in the solution of lower concentration, in general, are taller than those growing in the solutions of higher concentration.

The influence of total concentration upon height of plant when taken in connection with optimum and deficient nitrogen supply is indicated in figure 2, which shows a curve for each of the two measurements made on each plant, the upper curve being plotted from the last measurements taken. This curve is especially interesting since it shows the influence of nitrogen as a prime factor in growth in solutions which are of approximately the same concentration. Thus in I D 4 and I B 1, where the total concentrations are 3.14 g. and 3.06 g., the heights of the two plants are 91.5 cm. and 5.5 cm. Such a large difference can be due in this case only to the lack of nitrogen in I B 1, since there is present a considerable excess of the other nutrients required (pl. 7).

A study of the early and late height curves shows that the plant responded very early to the amount of salts available, as is indicated by the similarity of the early curve to that based upon the later measurements. The greatest final height is attained, as was to be expected, through the continuous growth of those plants which had sufficient nitrogen, while the growth of the under-nourished plant was decidedly retarded. Thus at the end of the growing season the differences in height between the two groups became more marked as the time of complete maturity drew near. Attention is called to this fact since it is not an uncommon practice in growing plants in water cultures to harvest them before maturity. While these plants might give an index of the influence of the culture solution on growth, they would not give a true value for the nutritive function of the solution, since increase might persist for a considerable time in solutions of optimum nutritive value while plants growing in an unfavorable medium would be practically at a standstill.

Dry Weight in Series I

A comparison of the curves for height (fig. 1) and for dry weight (fig. 3) shows that in a general way height is an index to the dry weight. This fact is more marked in this series than in either series II or III since the plants were more uniform throughout the series, being uniformly stocky where the height was above 40 cm. In the other groups some of the plants were

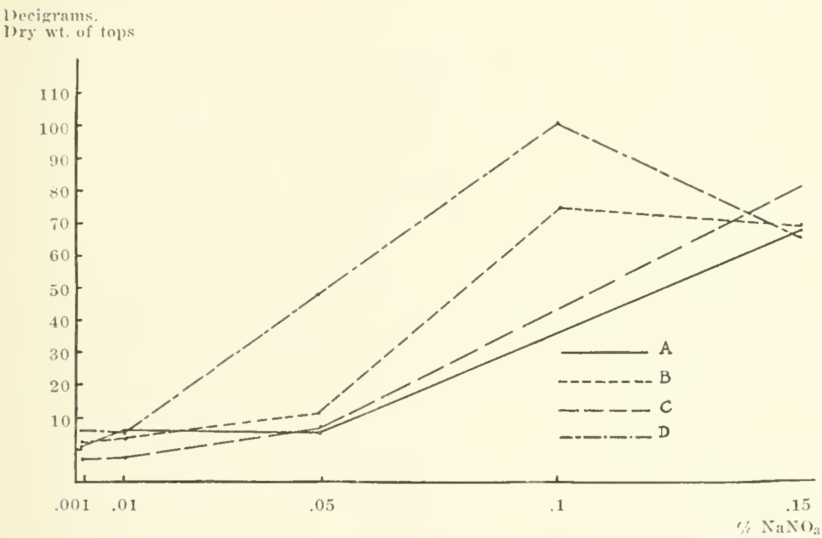

Fig. 3.—Graph showing influence of equal quantities of $NaNO_3$ in the different groups of series I upon dry weight of tops.

tall and very spindly (pl. 15), and there was a marked decrease in the length and width of leaf, which would, of course, lower the dry weight. The height measurements even on a plant of the habit of the tobacco cannot be taken alone as an indication of the nutritive value of a solution, a fact which has been shown to hold true to a much more noticeable extent in such plants as wheat, which will stool more in some cultures than in others without perceptible differences in height.

The effect of the concentration is evidenced in the curve for group D, which is much higher for plants 3 and 4 than for plants of like number in any other groups. Had it been possible to take

the dry weight for plant I C 4 this weight would probably have been slightly greater than that of I D 4 (see table 2), making the curves correspond to those for height.

THE INFLUENCE OF THE CULTURE SOLUTION ON FLOWER PRODUCTION

Our information concerning factors which may influence flower formation is very incomplete. Vochting[21] has demonstrated that light intensity is a factor in flower development in *Mimulus*, and numerous other plant physiologists have found that a more or less marked influence on flower formation could be correlated with some external factor. The relation to the formation of flowers of nutrient salts in the medium in which growth takes place seems never to have been studied in any thoroughgoing manner. Mobius[22] found that certain *Gramineae* flowered better on dry soil and on soil low in nutrient elements than on soil rich in nutrients and where water supply was abundant. Jost[23] thinks that the fact that root pruning increases flower production may be thus explained, since there is a lowering of the absorptive capacity of the tree for inorganic salts. There has been also a general opinion, which is not fully justified, that any condition which will cause marked vegetative development will retard flower production. The experiment herein reported has presented an opportunity for a study of the influence of the composition and concentration of the solution upon flower production.

In the plant used in this experiment the flowers fall soon after opening, leaving a scar upon the inflorescence stock.[24] At the end of the growing season the number of flowers produced by each plant was determined by counting these scars (see table 2). The total number of flowers produced by each plant is shown diagrammatically in figure 4.

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21 Vochting, Jahrb. f. wiss. Bot., vol. 25, p. 149, 1893.

22 Mobius, Beitr. z. Lehre v. d. Fortpflanzung d. Gewachse, Jena, 1897.

23 Jost, Lectures on plant physiology, p. 364, 1907.

24 Goodspeed and Ayres, Univ. Calif. Publ. Bot., vol. 5, no. 9, 1916.

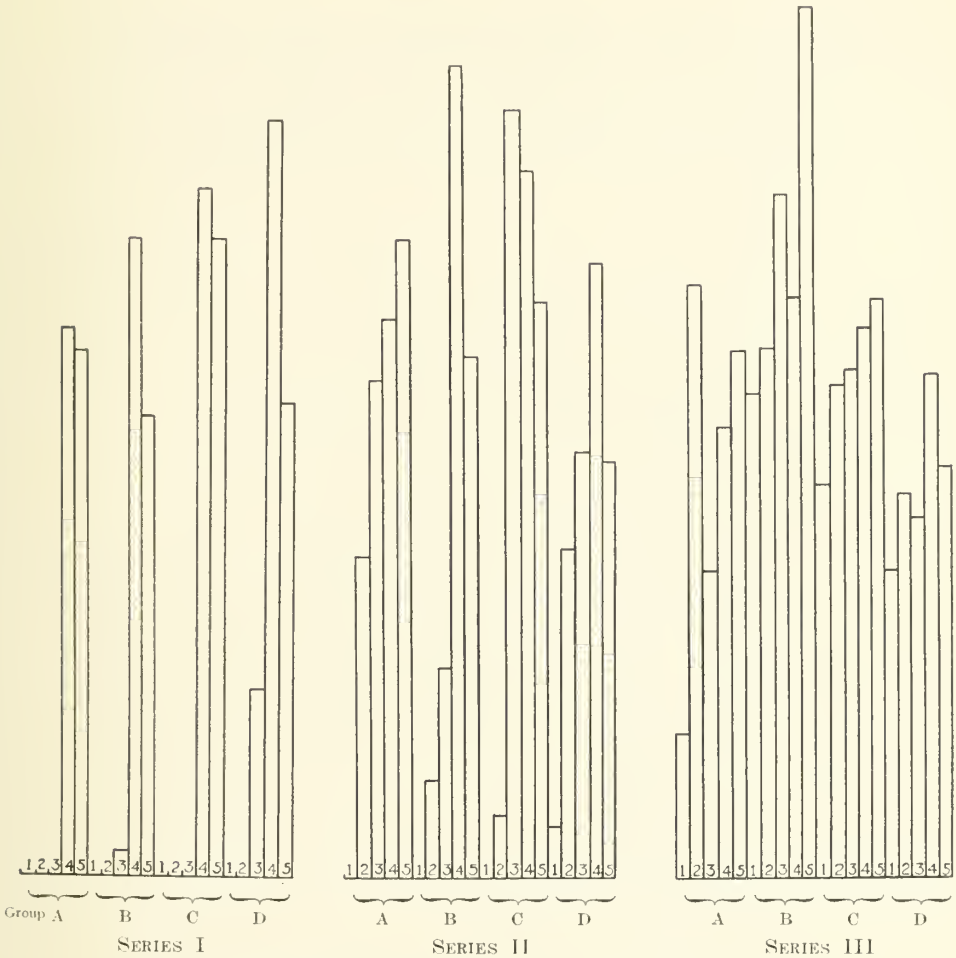

Fig. 4.—Diagrammatic representation of the number of flowers produced by each plant in series I, II, and III.

Flower Production in Series I

The nitrogen supply is seen to have a very definite influence upon flower production. In series I no flowers were produced by plants 1 and 2 of any group and in only two groups were any flowers produced by plant 3, showing definitely that unless nitrogen is present in excess of 0.05 per cent as $NaNO_3$ the undernourished tobacco plant will not flower. Flower production in

general corresponded to vegetative vigor, the plant exhibiting maximum vegetative growth producing the largest number of flowers. Here again the influence of the total concentration of the solution was apparent in the flower yield in the various groups, which increased as the concentration decreased.

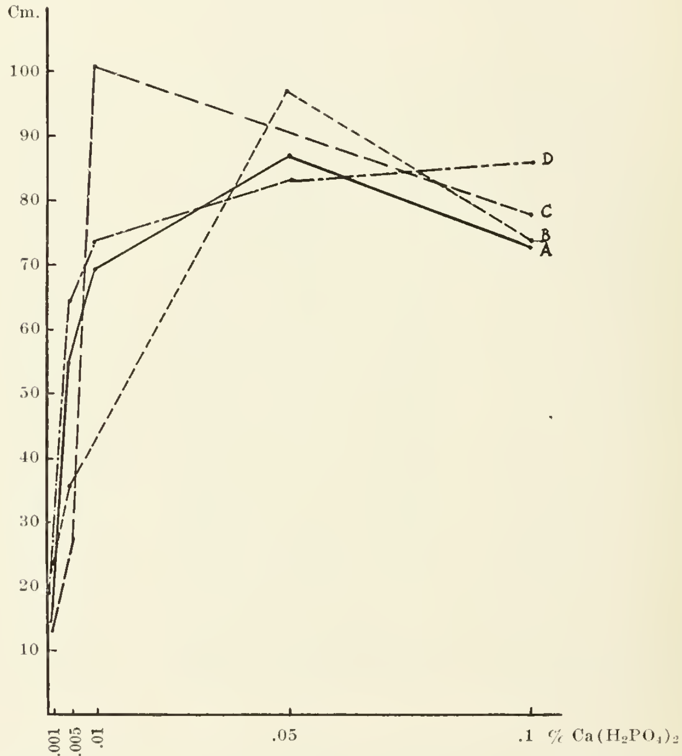

Fig. 5.—Graph showing the influence upon height of equal quantities of $Ca(H_2PO_4)_2$ in the different groups of series II.

PHYSIOLOGICAL EFFECT OF PHOSPHORUS

Distribution of Salts in Series II

In series II a study was made of the influence of phosphorus added as $Ca(H_2PO_4)_2$. This salt was present in the same quantity in all groups A, B, C, and D, the quantity in each of the pots 1 to 5 being 0.02 g. (.001 per cent), 0.1 g. (.005 per cent), 0.2 g. (.01 per cent), 1.0 g. (.05 per cent), 2.0 g. (.1 per cent),

respectively. The maximum weights of the other salts were $NaNO_3$, 3 g.; K_2SO_4, 2.4 g.; $MgSO_4$, 0.96 g., in group A, while the minimum quantities of these salts as added in group D were 0.75 g., 0.6 g., and 0.24 g., respectively. The total concentration in this series ranged from 1.61 g. to 6.38 g.

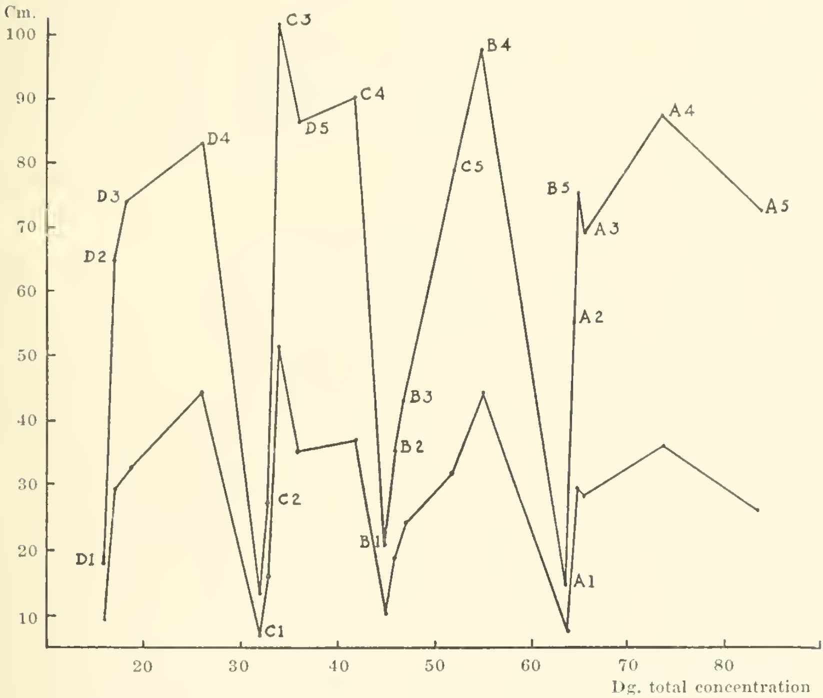

Fig. 6.—Graph showing the influence of total concentration upon height in series II.

Height in Series II

Figure 5 shows the height curves for the five plants of each of the four groups in this series. There is clear indication that the optimum phosphorus supply lies somewhere between .05 per cent and .01 per cent of $Ca(H_2PO_4)_2$, the height of plant 4 being greatest when all groups are considered. The difference in height between plants 4 and 5 is not great in any group. The effect of increasing the quantity of $Ca(H_2PO_4)_2$ is clearly seen in plants 1, 2, 3, and 4 of groups A, B, and D (pl. 8). The effect of total

concentration in this series is not so marked as in series I, but is slightly evidenced in the somewhat better growth of some of the plants in groups C and D as compared with plants in groups A and D (pl. 9). The height of the plants at two different periods in their growth was taken in this series at the same time that the measurements were taken in series I and plotted against total concentration (fig. 6). The total concentration of salts in the solution is here, as in series I, of secondary importance when one element is present in insufficient amount, as will be seen (pl. 6) when plant II C 1 (3.20 g.) is compared with II C 3

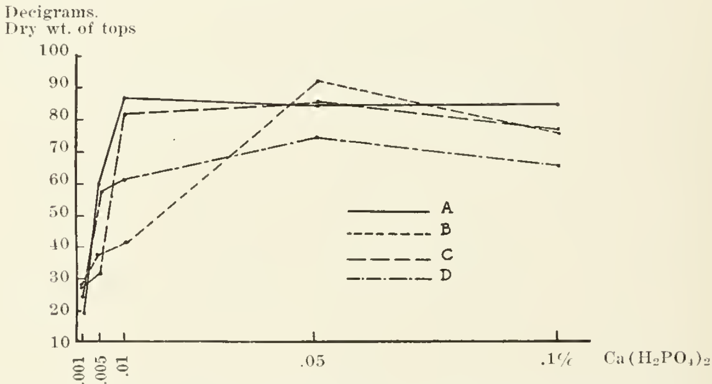

Fig. 7.—Graph showing the influence on dry weight of tops of equal quantities of $Ca(H_2PO_4)_2$ in the different groups of series II.

(3.38 g.). While the total concentration is practically the same and the total quantity of each of the other salts is the same the $Ca(H_2PO_4)_2$ in II C 3 is ten times the quantity of the same salt in II C 1.

Dry Weight in Series II

A comparison of height (fig. 5) and dry weight curves (fig. 7) for tops in this series shows that height here is not an accurate index to dry weight. Thus group A gave the greatest total dry weight, while the greatest total height of plants occurred in group D, a fact which is explicable since very serious injury resulting in a spindly habit was shown by many plants in the D group, as will be pointed out later in the discussion of injury due to the improper balance of salts in the solution.

Flower Production in Series II

The total number of flowers produced in this series was larger than in series I, due largely to the fact that there was less stunted growth in plants 1, 2, and 3 of each group, for which an ample supply of nitrogen was available. Plants II A 1, II B 1, and II C 1 did not produce any flowers. The greatest number of flowers was formed in group C and the greatest yield of any one plant was given by II B 5. The flower yield in each group is definitely related to the general character of the plant as mentioned above in connection with series I.

PHYSIOLOGICAL EFFECT OF POTASSIUM

Distribution of Salts in Series III

The plants in series III were grown to study the physiological influence of various quantities of potassium added as K_2SO_4 in the presence of a sufficient supply of other nutrient salts, following the same plan as outlined above for the variation of nitrogen and phosphorus in series I and II. K_2SO_4 was present in the same weight in each of the four groups A, B, C, and D, the quantities added to each of the pots 1 to 5 being 0.02 g. (.001 per cent), 0.1 g. (.005 per cent), 0.2 g. (.01 per cent), 1.0 g. (.05 per cent), and 2.0 g. (.1 per cent). The maximum weights of the other salts were $NaNO_3$, 3 g.; $Ca(H_2PO_4)_2$, 1.2 g.; $MgSO_4$, 0.96 g., in group A. In group D the minimum quantities of these salts were 0.75 g., 0.3 g., and 0.24 g., respectively. The total concentration in this series varied from 1.31 g. to 7.16 g.

Height in Series III

No plants in this series were less than 50 cm. high, due to the fact that the two nutrient elements, nitrogen and phosphorus, which in the order named are of first importance as growth factors, were present in sufficient quantity to insure considerable growth (pl. 7). Only a small quantity of K_2SO_4 (.005 to .01 per cent) was required in this series to give plants of maximum height, hence the curves show a downward trend in all plants after either plant 2 or plant 3 in each group (fig. 8, also pl. 12). Thus it is evident that there is a toxic effect of an excess of potassium, irrespective of the total concentration of the solution.

The influence of total concentration is again plainly seen in this series. Plate 13 shows plant 1 of each of the groups A, B, C, and D. As the total concentration decreases from A to C there is a steady increase in the vigor of the plant as judged by height. Curves in figure 9 indicate this general tendency to an increase of height with a decrease in the total concentration of the solution.

Dry Weight in Series III

As in series I and II, the dry-weight curves (fig. 10) do not correspond with the height curves (fig. 8). The greatest dry weight of any plant was that of III A 4, which was not so tall as the other plants of like number. The low dry weight of III B 4 is especially noticeable. A comparison of the two dry-weight curves for the A and B groups shows a very peculiar effect of K_2SO_4 in solutions of different balance. In each case where the group A curve is high, the group B curve is low, a fact which also applies to plants 3, 4, and 5 in the A and C groups. That this should occur with such regularity is rather remarkable and no satisfactory explanation can as yet be found to account for this situation. It is evident that the physiological balance of salts in the solution is dependent upon the concentration, as has been shown by McCool,[25] Gile,[26] Tottingham,[27] and Shive.[28]

Flower Production in Series III

The more vigorous growth of plants in this series gave a greater total yield of flowers than either of the other two series. This was to be expected from the result of series I and II, where the flower yield was shown to be definitely related to the general vigor of the plants. The production of flowers in this series differs, however, from that in the other series. An increase of K_2SO_4, while in general depressing the total height of the plant, when added in excess of .01 per cent gave a higher flower yield. Thus in group C there is steady increase in the number of flowers produced which corresponds to the increase of K_2SO_4. The

[25] McCool, Cornell Agric. Exp. Sta. Mem., vol. 2, pp. 121–170, 1913.
[26] Gile, Porto Rico Agric. Exp. Sta. Bull. 12.
[27] *Loc. cit.*
[28] *Loc. cit.*

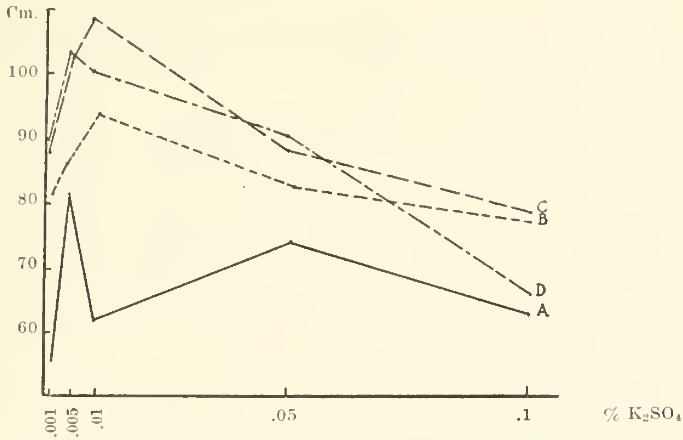

Fig. 8.—Graph showing the influence upon height of equal quantities of K_2SO_4 in the different groups of series III.

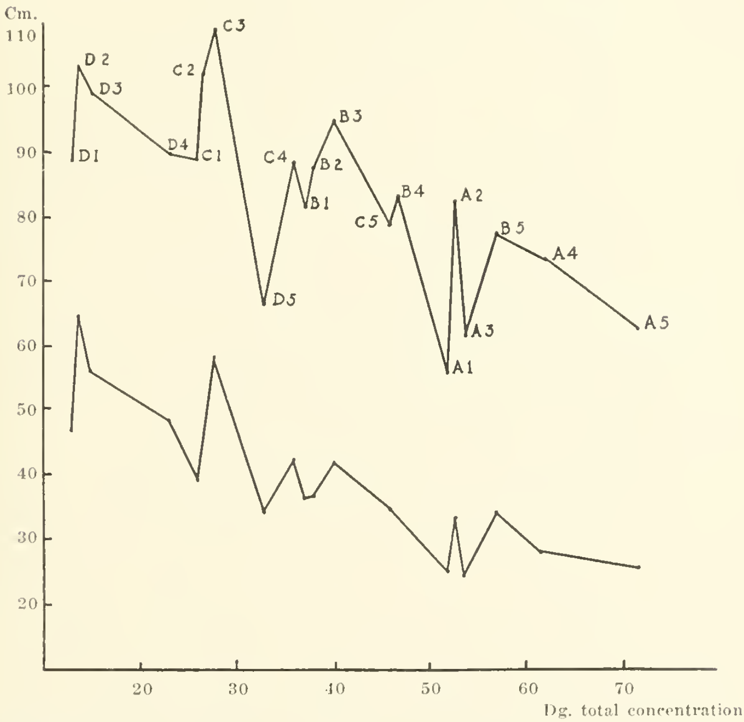

Fig. 9.—Graph showing the influence upon height of total concentration in series III.

greatest flower production occurred in group B, and plant 5 of this group produced a larger number of flowers than any other plant in any series.

INJURY DUE TO EXCESS OR DEFICIENCY OF NUTRIENT SALTS

The deficiency or excess of certain elements will cause injury which is very characteristic. Gris as early as 1843 showed that chlorosis was caused by a lack of iron in the nutrient solution. Nitrogen starvation likewise has long been known to cause chlorosis, a condition which may also result from an excess of soluble

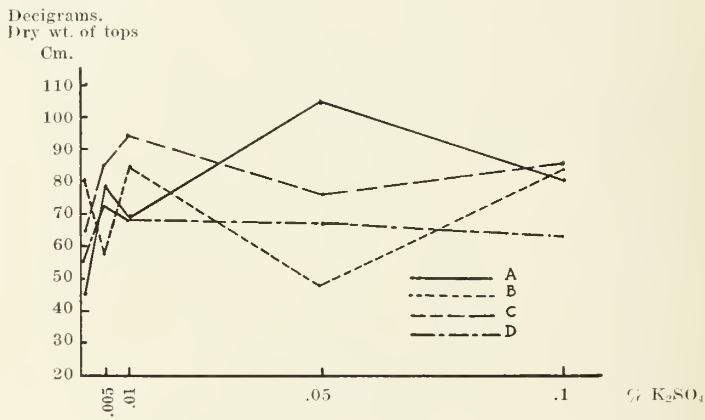

Fig. 10.—Graph showing the influence upon dry weight of tops of equal quantities of K_2SO_4 in the different groups of series III.

phosphate.[29] Magnesium starvation results in injury to the chlorophyll bodies, and in excess is harmful unless antagonized by calcium.[30] Other physiological disturbances not so well established as these mentioned have been considered to be associated with a deficiency or excess of nutrient elements.

The most marked indication of the fact that certain cultures in this experiment did not furnish a normal medium for growth was seen in the chlorosis which is so characteristic of plants grown in solutions which are deficient in nitrogen. This type of injury was uniformly present in all cultures containing 1.0 g. or less of $NaNO_3$, but was especially marked in series I, plants 1, 2, and 3, of all groups. It is not possible to draw a sharp

[29] Crone, Sitzungsber Neiderrhein. Ges. Nat.- und Heilk, Bonn, 1902, pp. 167–173.

[30] Loew and May, U. S. Dept. Agric. Bur. Plant Ind. Bull. 1, 1901.

line which will clearly segregate the injury to the various plants of a large series of this kind into well-defined groups since there is always more or less overlapping. An attempt was made, however, to divide the plants into groups which would show in each case a characteristic type of injury.

(*a*) This group was made up of plants which were very much stunted, being less than 8 cm. in height and in every case showed a marked chlorosis which was clearly attributed to a low supply of nitrogen. The plants in this group were I A 1, I A 2, I A 3, I B 1, I B 2, I B 3, I C 1, I C 2, I C 3, I D 1.

(*b*) This group was somewhat taller, from 13 to 21 cm. high, but clearly stunted in growth. These plants showed less chlorosis, since nitrogen was present in sufficient quantity to provide close to the optimum supply in all cultures with the exception of II D I and I D 2, where there was a distinct chlorosis due to the low nitrogen supply. Plants showing this type of injury were II A 1, II B 1, II C 1, II D 1, I D 2.

(*c*) Plants in this group showed a more serious type of injury than any of the other plants. They were more than 40 cm. in height, but were very spindly (pl. 15). The whole plant showed marked chlorosis, which affected the lower leaves most severely and soon resulted in their death. This type of plant was found in cultures I D 3, II B 2, II B 3, II C 2, II D 2, II D 3, II D 4, III D 1, III D 2, III D 3, III D 4, and III D 5.

(*d*) The plants of this group were decidedly more vigorous than those of the preceding groups, as indicated by their increased height and better color. Indeed, they seemed to be perfectly normal. The following cultures were classed in this group: I C 4, I D 4, II C 3, II C 4, II D 5, III A 1, III A 2, III A 3, III B 1, III B 2, III B 3, III C 1, III C 2, III C 3, III C 4, III C 5. The following plants were even better in appearance than those just named: I A 4, I A 5, I B 4, I B 5, I C 5, I D 5, II A 2, II A 3, II A 4, II A 5, II B 4, II B 5, II C 5, III A 4, III A 5, III B 4, III B 5.

A study of the above grouping indicates that chlorosis was present wherever the nitrogen content was low, as was to be expected. The spindly growth characteristic of groups II D and III D may also be due to the low supply of nitrogen. It seems

that the injury which was so marked in series II must be in some way associated with the calcium-magnesium content in solutions which were not properly balanced. No definite calcium-magnesium ratios can be found which are responsible for the injury which occurred in this series. Twenty different calcium-magnesium ratios ranging from 0.035 to 3.54 occur in the series, and both plants which were normal and plants which were seriously injured were found in cultures in which the calcium-magnesium ratio was low as well as in cultures where this ratio was high. No definite conclusions can be drawn in this connection, however, since the other variables present complicate the situation so that the injury cannot be said with certainty to be associated with an improper balance between the calcium and magnesium.

TABLE 3

SUMMARY OF COMPLETE EXPERIMENTS

Grouped in such a manner that comparison can be made with special reference to the influence of concentration and balance of the solution upon crop and flower production. The calculation of the per cent total concentration is based on the assumption that the salts are all dissolved in the quantity of water held by 2000 grams of sand when saturated. To get this value in parts per million, multiply the total concentration in grams by 227.2. The real concentration would be much greater than these values would indicate, since the sand was not kept saturated.

SERIES I

	$NaNO_3$, grams	$NaNO_3$, per cent	$Ca(H_2PO_4)_2$ grams	K_2SO_4 grams	$MgSO_4$ grams	Total, grams	Total concentration, per cent in solution	Height, cm.	Tops (dry), grams	Number of flowers
IA1	.02	.001	1.2	2.4	.96	4.58	1.04	2.5	1.12	0.
IB1	.02	.001	.8	1.6	.64	3.06	.69	5.5	1.29	0.
IC1	.02	.001	.6	1.2	.48	2.30	.52	3.5	.74	0.
ID1	.02	.001	.3	.6	.24	1.16	.26	6.5	1.65	0.
IA2	.2	.01	1.2	2.4	.96	4.76	1.08	4.5	1.6	0.
IB2	.2	.01	.8	1.6	.64	3.24	.73	3.5	1.40	0.
IC2	.2	.01	.6	1.2	.48	2.48	.56	2.5	.79	0.
ID2	.2	.01	.3	.6	.24	1.34	.30	17.5	1.53	0.
IA3	1.0	.05	1.2	2.4	.96	5.56	1.26	8.	1.56	0.
IB3	1.0	.05	.8	1.6	.64	4.04	.91	8.	2.17	1.
IC3	1.0	.05	.6	1.2	.48	3.28	.74	4.5	1.65	0.
ID3	1.0	.05	.3	.6	.24	2.14	.48	59.5	5.86	8.5
IA4	2.0	.1	1.2	2.4	.96	6.56	1.35	57.5	......	25.5
IB4	2.0	.1	.8	1.6	.64	5.04	1.14	78.	8.57	29.
IC4	2.0	.1	.6	1.2	.48	4.28	.97	94.	......	31.
ID4	2.0	.1	.3	.6	.24	3.14	.71	91.5	11.12	34.5
IA5	3.0	.15	1.2	2.4	.96	7.56	1.71	45.5	7.83	24.
IB5	3.0	.15	.8	1.6	.64	6.04	1.37	49.	7.96	21.
IC5	3.0	.15	.6	1.2	.48	5.28	1.20	74.	9.24	29.
ID5	3.0	.15	.3	.6	.24	4.14	.94	66.	7.60	21.5

Series II

	$Ca(H_2PO_4)_2$, grams	$Ca(H_2PO_4)_2$, per cent	$NaNO_3$ grams	K_2SO_4 grams	$MgSO_4$ grams	Total, grams	Total concentration, per cent in solution	Height, cm.	Tops (dry)	Number of flowers
IIA1	.02	.001	3.	2.4	.96	6.38	1.45	15.	2.09	0.
IIB1	.02	.001	2.25	1.6	.64	4.51	1.02	21.	2.71	0.
IIC1	.02	.001	1.5	1.2	.48	3.20	.72	13.5	2.73	0.
IID1	.02	.001	.75	.6	.24	1.61	.36	18.	2.47	2.5
IIA2	.10	.005	3.	2.4	.96	6.46	1.46	55.	6.21	14.5
IIB2	.10	.005	2.25	1.6	.64	4.59	1.04	35.5	3.82	4.5
IIC2	.10	.005	1.5	1.2	.48	3.28	.74	27.5	3.22	3.
IID2	.10	.005	.75	.6	.24	1.69	.38	64.5	5.83	15.
IIA3	.20	.01	3.	2.4	.96	6.56	1.49	69.5	8.75	22.5
IIB3	.20	.01	2.25	1.6	.64	4.69	1.06	43.	4.11	9.5
IIC3	.20	.01	1.5	1.2	.48	4.18	.94	101.	8.20	17.5
IID3	.20	.01	.75	.6	.24	2.59	.58	74.	6.27	16.
IIA4	1.0	.05	3.	2.4	.96	7.36	1.67	87.	8.58	25.5
IIB4	1.0	.05	2.25	1.6	.64	5.49	1.24	97.	9.3	37.
IIC4	1.0	.05	1.5	1.2	.48	4.18	.95	90.	8.66	32.
IID4	1.0	.05	.75	.6	.24	2.59	.58	83.5	7.60	28.
IIA5	2.0	.1	3.	2.4	.96	8.36	1.90	73.	8.60	29.
IIB5	2.0	.1	2.25	1.6	.64	6.49	1.47	74.5	7.76	23.5
IIC5	2.0	.1	1.5	1.2	.48	5.18	1.17	78.	7.88	26.5
IID5	2.0	.1	.75	.6	.24	3.59	.81	86.	6.75	19.

Series III

	K_2SO_4, grams	K_2SO_4, per cent	$NaNO_3$ grams	$Ca(H_2PO_4)_2$ grams	$MgSO_4$ grams	Total, grams	Total concentration, per cent in solution	Height, cm.	Tops (dry)	Number of flowers
IIIA1	.02	.001	3.	1.2	.96	5.18	1.17	56.5	4.65	6.5
IIIB1	.02	.001	2.25	.8	.64	3.71	.84	81.5	8.18	22.
IIIC1	.02	.001	1.5	.6	.48	2.60	.59	89.	6.58	18.
IIID1	.02	.001	.75	.3	.24	1.31	.29	89.	5.56	14.
IIIA2	.1	.005	3.	1.2	.96	5.26	1.19	82.5	7.88	27.
IIIB2	.1	.005	2.25	.8	.64	3.79	.86	87.	5.87	24.
IIIC2	.1	.005	1.5	.6	.48	2.68	.60	102.	8.57	22.5
IIID2	.1	.005	.75	.3	.24	1.39	.31	103.5	7.27	17.5
IIIA3	.2	.01	3.	1.2	.96	5.36	1.21	62.	6.97	14.
IIIB3	.2	.01	2.25	.8	.64	3.89	.88	94.5	8.4	31.
IIIC3	.2	.01	1.5	.6	.48	2.78	.63	109.	9.4	23.
IIID3	.2	.01	.75	.3	.24	1.49	.33	100.5	6.9	16.5
IIIA4	1.0	.05	3.	1.2	.96	6.16	1.40	74.	10.53	20.5
IIIB4	1.0	.05	2.25	.8	.64	4.69	1.06	83.	4.86	26.5
IIIC4	1.0	.05	1.5	.6	.48	3.58	.81	88.5	7.66	25.
IIID4	1.0	.05	.75	.3	.24	2.29	.52	90.	6.75	23.
IIIA5	2.0	.1	3.	1.2	.96	7.16	1.62	63.	8.11	24.
IIIB5	2.0	.1	2.25	.8	.64	5.69	1.29	77.5	8.42	39.5
IIIC5	2.0	.1	1.5	.6	.48	4.58	1.04	79.	8.68	26.5
IIID5	2.0	.1	.75	.3	.24	3.29	.74	66.5	6.36	19.

THE ABSORPTION OF SALTS FROM THE CULTURE MEDIUM

The absorption by plants of salts from a solution is no doubt intimately related to the composition of the solution, since the intake of inorganic salts occurs only when the concentration of the solute outside the permeable protoplast is greater than that within. Hence the total osmotic concentration of a solution may affect the intake and storage of the salts from the solution.[31] The quantity of salts which are absorbed by the plant may also vary with the qualitative composition of the solution. Thus True and Bartlett[32] have shown that absorption from a solution of two or of three salts is more rapid than from a solntion containing a single salt. It is evident that the factors which regulate absorption are very complex, and that this complexity increases with an increase in the number of different anions and cations in the solution. It is further evident that two methods may be followed with a view to ascertaining the quantities of salts absorbed. The ash of the plants may be analyzed or the residue of salts remaining in the culture may be determined. It has seemed desirable to attempt a study of absorption in the present case by means of the latter method.

Method of Analysis

The small quantities of salts added to each pot made the acid-extraction method undesirable, since the large quantities of sand required to give weighable precipitates would have been extremely hard to dehydrate, thus introducing a considerable source of error. For this reason the colorimetric method of analysis[33] was used in this work. An exception was made in the determination of calcium, which was made by the usual volumetric method. The sulphur was determined gravimetrically as $BaSO_4$. A water extract was prepared from 250 g. of sand by leaching with successive small portions of distilled water until

[31] Livingston, The rôle of diffusion and osmotic pressure in plants, Chicago, 1903.

[32] True and Bartlett, U. S. Dept. Agric. Bur. Plant Ind. Bull. 231, 1912, and Am. Jour. Bot., vol. 2, pp. 255–278, 311–323, 1915, vol. 3, pp. 47–58, 1916.

[33] Schreiner and Failyer, U. S. Dept. Agric. Bur. Soils, Bull. 31, 1906.

500 c.c. had been used. The filter containing the sand was then allowed to stand for about fifteen hours, and the sand was leached with another 500 c.c. portion of water. The filtrate was evaporated to dryness, the residue dehydrated at 100° C, and strongly ignited in a platinum dish to destroy organic matter. The residue was then dissolved in hot water and made up to definite volume from which aliquot portions were taken for analysis. A 2000 g. sample of the washed sand used in the experiment gave by this method the following analysis:

N	K	P	Mg	Ca	S
00.	33.6	5.2	66.4	2.4	15.6 milligrams

In this analysis, as well as in all the following analyses, the statement made is for the total weight in milligrams of the element contained in 2000 g. of sand, which was the quantity contained in each pot. Table 4 gives a summary of the analysis of each of the sixty samples of sand used. The total quantity of each element present, calculated from the quantities of salts added plus the quantity in the original sand, is given, as well as the number of milligrams of the element missing from the pot at the end of the growing season. This latter value is the difference between the total weight of the elements present and the residue as shown by the analysis of the water extract. The difference thus obtained represents the quantity of the element absorbed by the plant and adsorbed by the sand particles. It must be admitted that it is not known just how great a factor adsorption may be in the case of this sand.

Discussion of Results

In series I no nitrogen as nitrate remained in pots 1, 2, 3, and 4 of groups A, B, and C. In group D there is a small residue of nitrogen in spite of the fact that the total crop production was greatest in this group. The concentration of the solution clearly affects the economical use of nitrogen, a fact which in general is also indicated in series II and in series III. It is especially noticeable that there is a much larger quantity of nitrogen left in series III D than in either series I D or II D. The total crop production for group III D was better than that of the D group

TABLE 4

SHOWING IN MILLIGRAMS THE WEIGHT OF EACH OF THE ELEMENTS N, P, K, MG, CA, AND S IN EACH POT (2000 GRAMS OF SAND) AT THE BEGINNING OF THE EXPERIMENTS AND THE WEIGHT OF EACH ELEMENT REMAINING AT THE END OF THE GROWING SEASON. THE DIFFERENCE REPRESENTS THE WEIGHT OF THE ELEMENT USED IN THE GROWTH OF THE PLANT OR HELD BY ADSORPTION BY THE SAND PARTICLES.

(In the following table the roman numerals indicate the series numbers, and the letters are those of the corresponding groups.)

	N total	N remaining	N difference	P total	P remaining	P difference	K total	K remaining	K difference	Mg total	Mg remaining	Mg difference	Ca total	Ca remaining	Ca difference	S total	S remaining	S difference	Dry weight, grams
IA1	3.29	0.0	3.29	300.3	6.2	294.1	572.3	81.6	490.7	160.9	71.2	89.7	192.8	1.6	191.2	581.1	23.6	557.5	1.12
IA2	32.9	0.0	32.9	300.3	7.8	292.5	572.3	91.2	481.1	160.9	44.8	116.1	192.8	6.4	186.4	581.1	32.4	548.7	1.60
IA3	164.6	0.0	164.6	300.3	6.2	294.1	572.3	94.4	457.9	160.9	71.2	89.7	192.8	7.2	185.6	581.1	39.5	541.6	1.56
IA4	329.3	0.0	329.3	300.3	8.0	292.3	572.3	83.2	489.1	160.9	71.2	89.7	192.8	13.6	179.2	581.1	54.3	526.8	......
IA5	493.9	20.3	473.6	300.3	9.6	290.7	572.3	76.8	495.5	160.9	64.0	96.9	192.8	9.6	183.2	581.1	31.3	549.8	7.83
IB1	3.29	0.0	3.29	201.9	7.8	194.1	392.8	81.6	311.2	129.4	65.6	63.8	129.3	8.0	128.5	391.3	30.2	361.1	1.29
IB2	32.9	0.0	32.9	201.9	2.6	199.3	392.8	52.8	340.0	129.4	61.2	68.2	129.3	12.8	116.5	391.3	23.6	367.7	1.4
IB3	164.6	0.0	164.6	201.9	5.7	196.2	392.8	60.8	332.0	129.4	71.2	58.2	129.3	18.4	110.9	391.3	34.5	356.8	2.17
IB4	329.3	0.0	329.3	201.9	5.7	196.2	392.8	36.0	356.8	129.4	68.4	61.0	129.3	4.8	124.5	391.3	27.4	363.9	8.57
IB5	493.9	36.1	457.8	201.9	7.8	194.1	392.8	57.4	335.4	129.4	99.6	29.8	129.3	31.2	98.1	391.3	......	....	7.96
IC1	3.29	0.0	3.29	152.8	6.2	146.6	303.0	75.2	227.8	113.7	89.6	24.1	97.6	9.6	88.0	297.2	25.2	272.0	.74
IC2	32.9	0.0	32.9	152.8	5.0	147.8	303.0	80.0	223.0	113.7	106.8	6.9	97.6	19.2	78.4	297.2	38.4	258.8	.79
IC3	164.6	0.0	164.6	152.8	6.4	156.4	303.0	73.6	229.4	113.7	61.2	52.5	97.6	12.0	85.6	297.2	43.9	253.3	1.65
IC4	329.3	0.0	329.3	152.8	5.7	147.1	303.0	26.8	276.2	113.7	61.2	52.5	97.6	28.0	69.6	297.2	51.1	246.1	......
IC5	493.9	1.58	492.5	152.8	7.0	145.8	303.0	35.2	267.8	113.7	54.0	59.7	97.6	42.4	55.2	297.2	41.7	255.5	9.24
ID1	3.29	1.13	2.16	79.0	4.0	75.0	168.3	40.8	127.5	90.0	61.2	28.8	50.0	28.0	22.0	156.2	27.4	128.8	1.65
ID2	32.9	1.17	30.7	79.0	3.6	75.4	168.3	28.0	140.3	90.0	100.0	....	50.0	66.4	....	156.2	21.9	134.3	1.53
ID3	164.6	1.26	163.5	79.0	3.6	75.4	168.3	20.0	148.3	90.0	69.6	20.4	50.0	66.4	....	156.2	30.2	126.0	5.86
ID4	329.3	1.58	327.7	79.0	5.7	73.3	168.3	8.0	160.3	90.0	78.0	12.0	50.0	12.0	38.0	156.2	46.6	109.6	11.12
ID5	493.9	1.80	492.1	79.0	6.2	72.8	168.3	12.8	145.5	90.0	42.8	47.2	50.0	41.6	8.4	156.2	......	....	27.76
IIA1	493.9	1.67	492.2	10.1	2.6	7.5	572.3	38.4	533.9	160.9	78.0	82.9	5.6	22.4	....	581.1	21.4	559.7	2.09
IIA2	493.9	1.67	492.2	29.8	2.6	27.2	572.3	24.8	547.5	160.9	15.7	145.2	18.3	65.6	....	581.1	......	....	6.21
IIA3	493.9	27.1	466.8	54.3	6.5	47.8	572.3	56.0	516.3	160.9	126.8	34.1	34.1	12.8	21.3	581.1	68.5	512.6	8.75
IIA4	493.9	22.6	471.3	251.1	7.8	243.3	572.3	80.0	492.3	160.9	76.8	84.1	161.0	12.8	148.2	581.1	115.0	466.1	8.58
IIA5	493.9	1.58	492.3	497.1	9.6	478.5	572.3	80.0	492.3	160.9	91.2	69.7	319.7	25.6	294.1	581.1	......	....	8.60

	N total	N remaining	N difference	P total	P remaining	P difference	K total	K remaining	K difference	Mg total	Mg remaining	Mg difference	Ca total	Ca remaining	Ca difference	S total	S remaining	S difference	Dry weight, grams
IIB1	370.4	1.26	369.1	10.1	2.9	7.2	392.8	68.8	324.0	129.4	71.2	58.2	5.6	20.8	....	391.3	38.4	352.9.	2.71
IIB2	370.4	1.08	369.3	29.8	2.3	27.5	392.8	57.6	335.2	129.4	45.6	83.8	18.3	52.8	....	391.3	36.8	354.5	3.82
IIB3	370.4	.81	369.5	54.3	3.1	51.2	392.8	60.8	332.0	129.4	64.0	65.4	34.1	20.8	3.3	391.3	33.4	357.9	4.11
IIB4	370.4	.90	369.5	251.1	7.5	243.6	392.8	67.2	325.6	129.4	62.8	66.6	161.0	44.8	116.2	391.3	28.0	363.3	9.30
IIB5	370.4	1.35	369.0	497.1	8.6	488.5	392.8	86.4	306.4	129.4	64.0	65.4	319.7	41.6	278.1	391.3	29.6	361.7	7.76
IIC1	246.9	.63	246.3	10.1	3.1	7.0	303.0	72.0	231.0	113.7	48.4	65.4	5.6	44.8	....	297.2	32.9	264.3	2.73
IIC2	246.9	.90	246.0	29.8	2.3	27.5	303.0	70.4	232.6	113.7	56.8	56.9	18.3	70.4	....	297.2	27.4	269.8	3.22
IIC3	246.9	......	....	54.3	3.4	50.9	303.0	52.8	250.2	113.7	71.2	42.5	34.1	13.6	20.5	297.2	51.6	245.6	8.20
IIC4	246.9	.54	246.3	251.1	6.5	244.6	303.0	46.4	256.6	113.7	56.8	56.9	161.0	57.6	103.4	297.2	42.2	255.0	8.66
IIC5	246.9	1.39	245.5	497.1	7.5	489.6	303.0	33.6	269.4	113.7	74.0	39.7	319.7	24.8	294.9	297.2	19.7	277.5	7.88
IID1	123.5	.45	123.0	10.1	2.3	7.8	168.3	56.0	112.3	90.0	51.2	38.8	5.6	24.0	....	156.2	19.4	136.8	2.47
IID2	123.5	.81	122.7	29.8	2.6	27.2	168.3	32.0	136.3	90.0	56.8	33.2	18.3	12.8	5.5	156.2	19.4	136.8	5.83
IID3	123.5	.76	122.7	54.3	3.4	50.9	168.3	20.8	147.5	90.0	60.8	29.2	34.1	9.6	24.5	156.2	27.4	128.8	6.27
IID4	123.5	.45	122.0	251.1	3.6	247.5	168.3	38.4	129.9	90.0	78.0	12.0	161.0	8.0	153.0	156.2	20.8	135.4	7.60
IID5	123.5	.45	122.0	497.1	5.8	491.3	168.3	37.6	130.7	90.0	79.6	10.4	319.7	17.6	302.1	156.2	8.2	148.0	6.75
IIIA1	493.9	1.8	492.1	300.3	4.6	295.7	38.1	16.4	21.7	160.9	49.6	111.3	192.8	12.0	180.8	143.0	10.9	132.1	4.65
IIIA2	493.9	3.6	490.3	300.3	4.6	295.7	56.0	28.0	28.0	160.9	74.0	86.9	192.8	7.2	185.6	158.2	33.4	124.8	7.88
IIIA3	493.9	2.7	491.2	300.3	6.5	293.8	78.6	22.0	56.6	160.9	61.2	99.7	192.8	19.2	173.6	171.5	24.6	146.9	6.97
IIIA4	493.9	2.3	491.6	300.3	6.0	294.3	258.0	57.6	200.4	160.9	....	....	192.8	21.6	171.2	322.9	60.4	262.5	10.53
IIIA5	493.9	2.3	491.6	300.3	7.3	293.0	483.6	29.6	454.0	160.9	71.2	89.7	192.8	17.6	175.2	455.9	......	....	8.11
IIIB1	370.4	3.61	366.8	207.9	6.0	195.9	38.1	26.4	11.7	129.4	35.6	93.8	129.3	10.4	118.9	101.6	15.6	86.0	8.18
IIIB2	370.4	2.25	368.1	207.9	6.2	195.7	56.0	40.0	16.0	129.4	68.4	61.0	129.3	23.2	106.1	116.8	38.9	77.9	5.87
IIIB3	370.4	1.35	369.0	207.9	5.8	196.1	78.6	24.0	54.6	129.4	49.6	79.8	129.3	10.4	118.9	129.1	36.9	92.2	8.84
IIIB4	370.4	1.44	368.9	207.9	5.8	196.1	258.0	43.2	214.8	129.4	99.6	29.8	129.3	4.8	124.5	281.5	10.2	271.3	4.86
IIIB5	370.4	.85	369.5	207.9	5.0	196.9	483.6	67.2	416.4	129.4	96.8	32.6	129.3	8.0	121.3	414.5	59.8	344.7	8.82
IIIC1	246.9	.36	246.5	152.8	2.9	149.9	38.1	28.0	10.1	113.7	82.8	30.9	97.6	8.0	89.6	80.7	17.5	63.2	6.58
IIIC2	246.9	1.58	245.3	152.8	4.4	148.4	56.0	18.4	37.6	113.7	75.2	38.5	97.6	8.8	88.8	95.9	......	....	8.57
IIIC3	246.9	.77	246.1	152.8	3.8	149.0	78.6	35.2	43.4	113.7	91.2	22.5	97.6	7.2	90.4	109.2	28.5	81.7	9.40
IIIC4	246.9	.41	246.5	152.8	7.0	145.8	258.0	41.6	216.4	113.7	62.8	50.9	97.6	10.4	87.2	260.6	50.0	210.1	7.66
IIIC5	246.9	4.52	242.4	152.8	7.3	145.5	483.6	60.8	422.8	113.7	68.4	45.3	97.6	11.2	86.4	393.6	30.7	262.9	8.68
IIID1	123.5	4.52	118.9	79.0	5.8	73.2	38.1	18.4	19.7	90.0	48.4	41.6	50.0	7.2	42.8	49.5	28.0	21.5	5.56
IIID2	123.5	4.06	119.4	79.0	4.1	74.9	56.0	18.4	37.6	90.0	85.6	4.4	50.0	6.4	43.6	54.7	23.0	31.7	7.29
IIID3	123.5	3.16	120.3	79.0	6.0	73.0	78.6	17.6	61.0	90.0	68.4	21.4	50.0	9.6	40.4	78.0	19.7	58.3	6.96
IIID4	123.5	4.52	118.9	79.0	6.5	72.5	258.0	40.0	218.0	90.0	89.2	.8	50.0	7.2	42.8	229.4	29.1	200.3	6.75
IIID5	123.5	4.96	118.5	79.0	6.0	73.0	483.6	48.0	435.6	90.0	84.0	6.0	50.0	3.2	46.8	362.4	45.0	317.4	6.36

in either of the other series, a result which is explicable since nitrogen is a more important limiting factor than phosphorus, and phosphorus is in turn more important as a limiting factor in growth than potassium. Hence in a solution where nitrogen is deficient, and potassium and phosphorus present in optimum amounts, a smaller crop production results than is the case where phosphorus is the deficient factor. A deficiency of potassium does not so seriously affect the intake of other salts, with the result that a better crop is produced than is the case where phosphorus is the deficient factor.

The method of analysis which it was necessary to use makes the analytical values for phosphorus and magnesium rather unreliable. In series II, where phosphate was added in increasing quantities from pot 1 to pot 5 in each group, the analysis of the water extract shows the effect of this increment. It will be noticed that the analytical values are all of about the same order of magnitude, which may point strongly to adsorption by the sand. No general conclusion as to the adsorption of phosphorus and of magnesium can be drawn for the reasons above enumerated.

In the case of potassium the method of analysis was much more accurate. There is evidence in series I, groups A, B, C, and D, of an increase in the amount of potassium absorbed which in general seems to be related to the more vigorous growth resulting from the increasing quantities of nitrogen as added in these groups. A similar relation holds in the other two series, as will be seen from the ratios between potassium added and potassium remaining, which are higher where the nitrogen is added in large quantities than is the case where this element was present in small quantities. The high ratios of potassium added to potassium remaining after growth, therefore, usually occur where the dry weight is highest.

Not much can be said on the absorption of calcium. In series I it is noticeable that the quantity of calcium remaining, as compared in the four groups of this series, bears an inverse relation to the calcium added. Less calcium is absorbed from the solutions of low total concentration than from those which have a high concentration. Since the crop production was

greater in group D, the calcium must have been used with greater economy in this group where the total concentration was low.

The large number of variables which are present in each of the solutions make accurate deductions concerning the exact relation between any element and the growth of the plant almost impossible. In fact, growth has been shown to be influenced not by one factor alone but by combinations of factors.

GENERAL DISCUSSION

It is evident, as noted above, that the large number of variables present in an experiment of this character so complicates the situation that definite conclusions are drawn only with considerable difficulty. Inorganic salts can be used by the plant only from solution. The complexity of this solution increases with the number of ions, which must be rather large since the plant cannot make normal growth unless certain ions are present. To further complicate the situation, all the salts may be available which are required for growth, but the unbalanced condition of the solution may cause injury to the growing plant.[34] This condition of balance, in turn, seems to be related to the total concentration of the solution as well as to its qualitative composition.[35] In this connection it is important to note that if it were possible to keep the balance in the solution constant by renewal of salts, growth differences would be less marked than when the plant grows in a solution in which the balance is constantly changing due to absorption of ions by the plant.[36] All of the above points must be taken into consideration in any experimental work which is done in this field of investigation. The exact influence which the concentration of the solution has upon the complicated physiological processes concerned in plant nutrition is a problem which can be solved only by the gradual accumulation of a mass of evidence bearing upon the subject. The complexity of the whole problem is such as to require more than

[34] Loeb, Archiv. ges. Physiol., vol. 88, pp. 68–78, 1902, and Amer. Jour. Physiol., vol. 3, pp. 327–338, 1900; Osterhout, Science, n. s., vol. 35, pp. 112–115, 1912, and Jour. Biol. Chem., vol. 1, p. 363, 1906.

[35] Gile, *loc. cit.*

[36] Brenchley, Ann. Bot., vol. 30, pp. 77–90, 1916.

the evidence of a single set of experiments for proof. The evidence presented by the work herein reported is an addition to that already reported by other investigators, who have shown that the absorption is influenced to a more or less marked degree by the concentration of the solution. Conclusions which have been reached in regard to the effect of certain variables in this study must be understood to apply only in the case of the specific combinations of salts studied, and in connection with the growth of the tobacco plant in sand cultures.

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SUMMARY

Results are above given which deal with the influence of the composition and concentration of the nutrient solution on sixty different plants of an F_1 species-hybrid of *Nicotiana*.

1. 2000 g. of washed sand of known composition was used as a culture medium for each plant.

2. The salts used were $NaNO_3$, $Ca(H_2PO_4)_2$, K_2SO_4, and $MgSO_4$.

3. The salts were so distributed as to give at least three important variables: first, as to a single nutrient salt; second, as to total concentration of salts; and third, as to the balance of salts in the solution.

4. The influence of the solution on the growth of the plant was judged by the following criteria: height, leaf length, leaf width, flower production, dry weight of tops.

5. Nitrogen is a more important growth-limiting factor than phosphorus, and phosphorus is, in turn, more important in this capacity than potassium.

6. The total concentration of the solution has a marked influence upon growth. Plants growing in solutions of low concen-

tration were in general superior to those grown in solutions of higher concentration.

7. Flower yield as well as vegetative vigor is influenced by the composition and concentration of the nutrient solution.

8. The physiological balance of salts in the solution is an important factor which must be taken into consideration in connection with the composition and concentration of the solution. Growth is influenced by a combination of all of these factors.

9. A quantitative analysis of the sand used in each pot was made after the plants were harvested.

10. Evidence of adsorption is seen in the results of the quantitative analysis of the water extract from the sand.

11. The concentration of the nutrient solution clearly affects the economical use of nitrogen.

12. High ratios of potassium added to potassium remaining after growth usually occur where the dry weight production is greatest.

13. Less calcium is absorbed from solutions of low total concentration than from those which have a high total concentration.

14. Calcium seems to be used with greater economy in solutions where the total concentration is low than in solutions in which the total concentration is high.

Transmitted April 21, 1916.

PLATE 5

TREATMENT

	$NaNO_3$ Grams	$Ca(H_2PO_4)_2$ Grams	K_2SO_4 Grams	$MgSO_4$ Grams	Total Grams
Pot 1D1	.02	.3	.6	.24	1.16
Pot 1D2	.2	.3	.6	.24	1.34
Pot 1D3	1.0	.3	.6	.24	2.14
Pot 1D4	2.0	.3	.6	.24	3.14
Pot 1D5	3.0	.3	.6	.24	4.14


4
3
2
1
I D 1
I D
I D 3
I D 4
I D 5

PLATE 6

TREATMENT

	$NaNO_3$ Grams	$Ca(H_2PO_4)_2$ Grams	K_2SO_4 Grams	$MgSO_4$ Grams	Total Grams
Pot IA4	2.0	1.2	2.4	.96	6.56
Pot IB4	2.0	.8	1.6	.64	5.04
Pot IC4	2.0	.6	1.2	.48	4.28
Pot ID4	2.0	.3	.6	.24	3.14


4
3
2
1
I A 4
I B 4
I C 4
I D 4

PLATE 7

TREATMENT

	$NaNO_3$ Grams	$Ca(H_2PO_4)_2$ Grams	K_2SO_4 Grams	$MgSO_4$ Grams	Total Grams
Pot IC1	.02	.6	1.2	.48	2.30
Pot ID3	1.0	.3	.6	.24	2.14
Pot IB1	.02	.8	1.6	.64	3.06
Pot ID4	2.0	.3	.6	.24	3.14


4
3
2
1
I C 1
I D 3
I B 1
I D 4

PLATE 8

TREATMENT

	$NaNO_3$ Grams	$Ca(H_2PO_4)_2$ Grams	K_2SO_4 Grams	$MgSO_4$ Grams	Total Grams
Pot IIB1	2.25	.02	1.6	.64	4.51
Pot IIB2	2.25	.1	1.6	.64	4.59
Pot IIB3	2.25	.2	1.6	.64	4.69
Pot IIB4	2.25	1.0	1.6	.64	5.49
Pot IIB5	2.25	2.0	1.6	.64	6.49


4
3
2

PLATE 9

TREATMENT

	$NaNO_3$ Grams	$Ca(H_2PO_4)_2$ Grams	K_2SO_4 Grams	$MgSO_4$ Grams	Total Grams
Pot IIA3	3.00	.2	2.4	.96	6.56
Pot IIB3	2.25	.2	1.6	.64	4.69
Pot IIC3	1.5	.2	1.2	.48	3.38
Pot IID3	.75	.2	.6	.24	1.79


4
3
2
1
II A 3
II B 3
II C 3
II D 3

PLATE 10

Treatment

	$NaNO_3$ Grams	$Ca(H_2PO_4)_2$ Grams	K_2SO_4 Grams	$MgSO_4$ Grams	Total Grams
Pot IIC1	1.5	.02	1.2	.48	3.20
Pot IIC3	1.5	.2	1.2	.48	3.38
Pot IIB1	2.25	.02	1.6	.64	4.51
Pot IIB4	2.25	1.0	1.6	.64	5.49


I C 1
II C 3
II B 1
4
3
2
1

PLATE 11

TREATMENT

	$NaNO_3$ Grams	$Ca(H_2PO_4)_2$ Grams	K_2SO_4 Grams	$MgSO_4$ Grams	Total Grams
Pot IB3	1.00	.8	1.6	.64	4.04
Pot IIB3	2.25	.2	1.6	.64	4.69
Pot IIIB3	2.25	.8	.2	.64	3.89


4
3
2
1
I B
II B 3
III B 3

PLATE 12

TREATMENT

	$NaNO_3$ Grams	$Ca(H_2PO_4)_2$ Grams	K_2SO_4 Grams	$MgSO_4$ Grams	Total Grams
Pot IIID1	.75	.3	.02	.24	1.31
Pot IIID2	.75	.3	.1	.24	1.39
Pot IIID3	.75	.3	.2	.24	1.49
Pot IIID4	.75	.3	1.0	.24	2.29
Pot IIID5	.75	.3	2.0	.24	3.29


4
3
2
III D 1
III D 2
III D 3
III D 4
III D 5

PLATE 13

TREATMENT

	$NaNO_3$ Grams	$Ca(H_2PO_4)_2$ Grams	K_2SO_4 Grams	$MgSO_4$ Grams	Total Grams
Pot IIA1	3.00	1.2	.02	.96	5.18
Pot IIIB1	2.25	.8	.02	.64	3.71
Pot IIIC1	1.5	.6	.02	.48	2.60
Pot IIID1	.75	.3	.02	.24	1.31


4
3
2
III A 1
III B 1
III C 1
III D 1

PLATE 14

TREATMENT

Plant growing in washed sand
Plant growing in soil

	$NaNO_3$ Grams	$Ca(H_2PO_4)_2$ Grams	K_2SO_4 Grams	$MgSO_4$ Grams	Total Grams
Pot IIIB2	2.25	.8	.1	.64	3.79


4
3
2
III
B
2

PLATE 15

Treatment

	$NaNO_3$ Grams	$Ca(H_2PO_4)_2$ Grams	K_2SO_4 Grams	$MgSO_4$ Grams	Total Grams
Pot ID2	.2	.3	.6	.24	1.34
Pot IID2	.75	.1	.6	.24	1.69
Pot IIID2	.75	.3	.1	.24	1.39


4
3
2
1
I D2
II D
III D2